The Segmentation of the Head in Squalus acanthias.

By

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With 13 Text-figures.

There are two views with regard to the segmentation of the head. One has arisen out of Balfour's (1) pioneer work, the other is due to Van Wijhe (18). They both agree on many points, and the difference between them lies in the interpretation of the numerical relations of the different segmented structures, as pointed out by Goodrich (8). In order that they may be compared, a short account of these views will now be given.

Balfour, in his classical 'Development of Elasmobranchs', expressed the opinion that the six visceral clefts are related to six consecutive somites situated dorsally and posteriorly to each respective cleft, the clefts being intersomitic. In front of the spiracle he recognized two somites (premandibular and mandibular), so that in all, from the anterior extremity to behind the last gill-slit, there are eight somites, of which the six posterior are simply and harmoniously related to six visceral arches and clefts.

The recognition of the nature of the cranial nerves is due to the work of Marshall and Van Wijhe. Five nerves are regarded as dorsal roots, viz. ramus ophthalmicus profundus, trigeminal, facial, glossopharyngeal, and vagus, the latter being really compound and probably representing four segments. There are then eight dorsal nerve elements, and if each is related to

one of Balfour's eight somites the following relations will result, as shown in Table I (ventral roots also included).

This is the theory which has grown out of Balfour's work, and the somites bearing the relations described above may be called Balfour's somites. Among the supporters of this view are Ziegler (**19**), Koltzoff (**10**), Goodrich (**8**).

Table I.

Segment.	*Dorsal Nerve.*	*Ventral Nerve.*	*Somite.*	*Visceral Arch.*	*Visceral Cleft.*
1	R.O.P.	Oculomotor	Premandibular	—	—
2	Trigeminal	Patheticus	Mandibular	Mandibular	Spiracle
3	Facial	Abducens	Hyoid	Hyoid	Gill-slit 1
4	Glossopharyngeal	—	4th	3rd	Gill-slit 2
5	Vagus 1	Hypoglossus	5th	4th	Gill-slit 3
6	Vagus 2	Hypoglossus	6th	5th	Gill-slit 4
7	Vagus 3	Hypoglossus	7th	6th	Gill-slit 5
8	Vagus 4	Hypoglossus	8th	7th	
9	1st Spinal	—	9th	—	

Table II.

Segment.	*Dorsal Nerve.*	*Ventral Nerve.*	*Somite.*	*Visceral Arch.*	*Visceral Cleft.*
1	R.O.P.	Oculomotor	Premandibular	—	—
2	Trigeminal	Patheticus	Mandibular	Mandibular	Lost
3	Facial	Abducens	Hyoid	Hyoid	Spiracle
4	Facial	—	4th	Hyoid	Gill-slit 1
5	Glossopharyngeal	—	5th	3rd	Gill-slit 2
6	Vagus 1	—	6th	4th	Gill-slit 3
7	Vagus 2	Hypoglossus	7th	5th	Gill-slit 4
8	Vagus 3	Hypoglossus	8th	6th	Gill-slit 5
9	Vagus 4	Hypoglossus	9th	7th	
10	1st Spinal	—	10th	—	

But the majority of authors have followed Van Wijhe (**18**) in the interpretation of the relations. He regards the facial nerve as really of double nature, the existing nerve being related to the fourth somite while the nerve of the third somite has either disappeared or become merged with that of the fourth. The relations of these somites (Van Wijhe's somites)

are shown in Table II. Braus (**2**), Hoffmann (**9**), Sewertzoff (**17**), and Neal (**11**) adopt this view.

The difference between the two interpretations is centred in the region of the spiracle and hyoid arch. On the first view all the segmented elements are harmoniously and consecutively related without gaps or discrepancies: on Van Wijhe's there is one somite too many in the region of the spiracle. For since the mandibular or second somite corresponds to the first (mandibular) visceral arch, if the second (hyoid) arch corresponds to the fourth somite, as Van Wijhe supposes, then the third somite has no arch or cleft. Van Wijhe suggests that these have been lost.

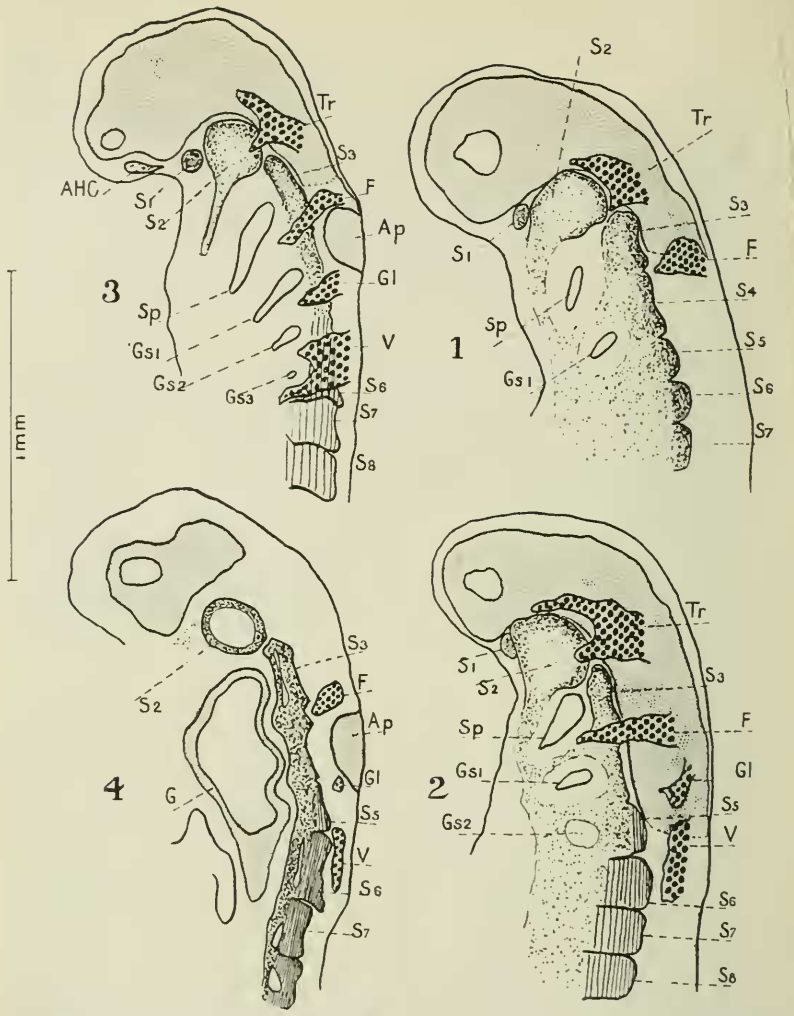
The question has been gone into thoroughly in the case of Scyllium canicula by Professor Goodrich (**8**), and it was at his suggestion that I undertook to investigate Squalus acanthias (Acanthias vulgaris) in order to see whether the conditions were similar in this related form.

The first part of this paper deals with the question of the correspondence in the region of the hyoid arch, and which somite forms the first permanent myotome. This is followed by a brief description of the occipital region, for the purpose of comparing the extent of the cranial region in Squalus and Scyllium.

The work was done in the Department of Comparative Anatomy at Oxford. To Professor Goodrich, for advice and encouragement, I wish to offer my grateful thanks. I also had the privilege of consulting Professor Neal in person and to him, for valuable assistance and material, I express my deep gratitude.

In a 4·5 mm. embryo (Text-fig. 1) reconstructed from longitudinal vertical sections all the somites of the head can be discerned. Two visceral clefts are present—spiracle and gill-slit 1 situated beneath the third and fourth somites respectively.

In the next stage (Text-fig. 2, 5 mm.) the second gill-slit has appeared beneath somite 5. Of the dorsal nerves trigeminal is related to the second somite, facial is situated between



Text-fig. 1.—Reconstruction of the head of an embryo of Squalus acanthias 4·5 mm. long seen from the left side.

Text-fig. 2.—Embryo 5 mm. long. First appearance of muscle-fibres in somite 5. The relation of somites to gill-slits and dorsal nerves is plainly seen.

Text-fig. 3.—Embryo 6 mm. long. The fifth somite is indistinct, the sixth is covered by the vagus except for the posterior dorsal corner, which begins to assume the hook-shaped appearance.

Text-fig. 4.—A single section through an embryo 5 mm. long, showing the single nature of the somite under the auditory capsule.

Explanation of Lettering.

Ab, Abducens nerve. *A.H.C.*, Anterior head cavity of Platt. *Ap.*, Auditory Placode. *A.S.*, Auditory Sac. *F*, Facial nerve. *G*, Gut. *Gl*, Glossopharyngeal nerve. *G.S.* 1-5, Gill-slits 1 to 5. *H*, Heart. *N*. 1–7, Neuromeres 1 to 7. *Oc*, Oculomotor nerve. *S*. 1–10, Somites 1–10. *Sp*, Spiracle. *Sp. Gn*. 2, Second Spinal Ganglion. *Tr*. Trigeminal nerve. *V*, Vagus nerve. *V*. 7–10, Ventral nerve-roots of segments 7 to 10. *V.C.L.*, Vena Capitis Lateralis.

somites 3 and 4, glossopharyngeal between 4 and 5. The rudiment of the first branch of the vagus overlies somite 5, which is the most anterior of the post-otic somites to develop muscle-fibres.

Text-fig. 3 shows clearly the relation of the vagus to the somites. It covers the posterior border of the fifth somite and most of the sixth. By tracing up through later stages I have arrived at the conclusion that it is the sixth somite which forms the first permanent myotome. For the greater part median to the vagus, its posterior dorsal corner is prolonged into a hook-shaped process which, lapping round the posterior edge of the vagus, extends forwards laterally to it. The hook-shaped process can be seen in an incipient condition in this (Text-fig. 3) and in subsequent stages; likewise that the sixth somite corresponds to the third gill-slit, which is of course related to the second branch of the vagus. There is also serial correspondence between spiracle, gill-slits 1 and 2, and the third, fourth, and fifth somites respectively. The establishment of this correspondence is important, for some authors (Dohrn, Froriep) have described a varyingly large number of somites under the auditory capsule. I am convinced that there is only one somite between the facial and the glossopharyngeal in Squalus. Text-fig. 4 is a drawing of a single section, and the region beneath the auditory capsule from two sections of another embryo is shown in Text-fig. 5 and under higher magnification. The peculiar nature of the posterior corner of the sixth somite also is shown.

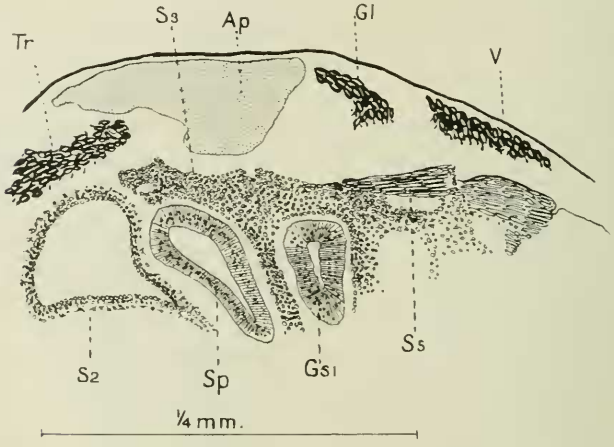
Each cleft lies between two visceral arches. The first or mandibular arch contains a prolongation of the second or mandibular somite. Therefore, since clefts and somites correspond, the next posterior visceral arch (hyoid or second) must correspond to the next somite (hyoid or third somite). This is corroborated by the fact that these two consecutive arches, first and second, are related to two consecutive dorsal nerves, trigeminal and facial. Similarly the third visceral arch corresponds to the fourth somite and the glossopharyngeal nerve. This interpretation implies that the dorsal roots are related to

the somites lying anterior to them, and it will be shown that this is the only view which avoids weighty assumptions and discrepancies.

As development proceeds the interpretation becomes more difficult, and for two reasons :

1. The fourth and fifth somites lose their distinctness and the fourth breaks up unrecognizably into mesenchyme. This is possibly due to the pressure of the auditory sac, which appears

TEXT-FIG. 5.

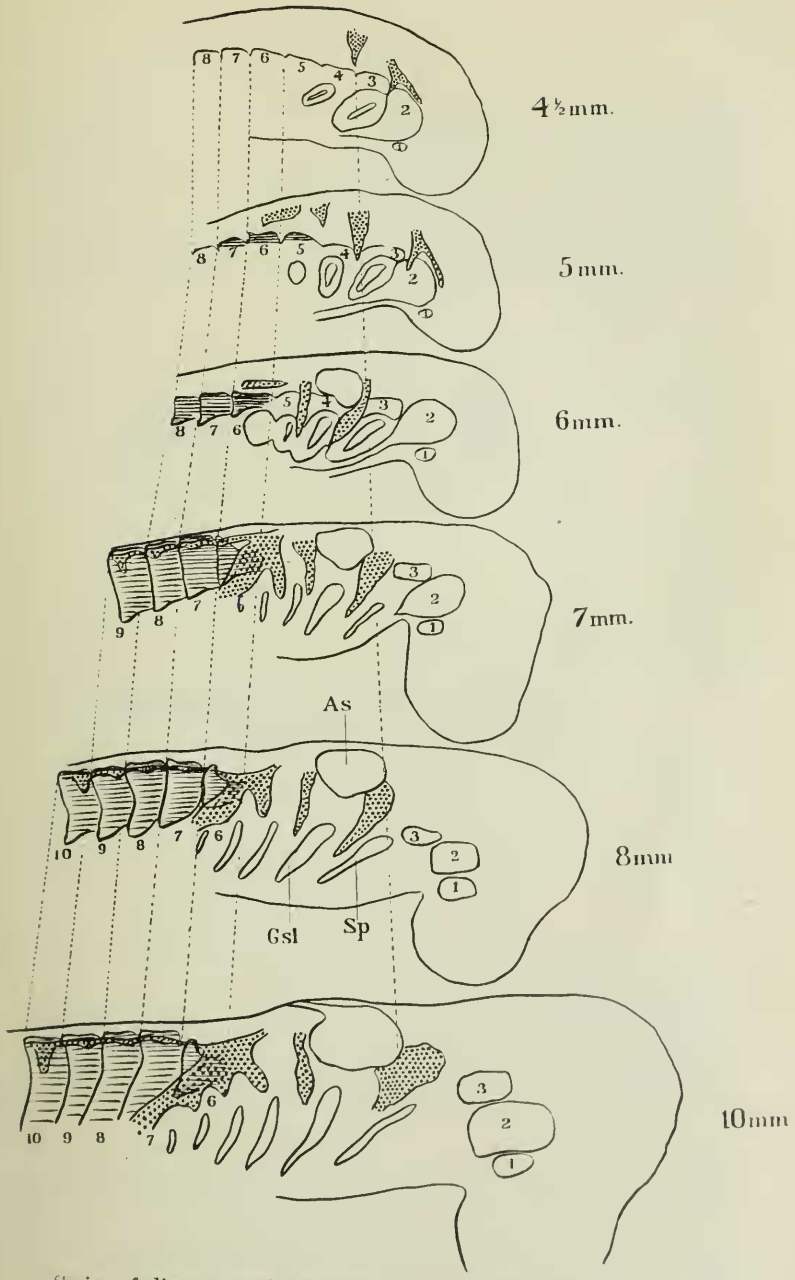


The somite beneath the auditory capsule.

between the facial and glossopharyngeal nerves, overlying the fourth somite. As the sac extends backwards the fifth somite also begins to break up, though some remnants of its muscle-fibres persist.

2. The somites appear in later stages to be situated more posteriorly with regard to the gill-slits. This is due partly to the development of the latter, which push them backwards, and partly to the fact that owing to the slight curvature which the head undergoes, the line of mesodermic somites finds itself situated on the outer side of the circumference of this curvature. Since the centre region of the head mesoderm (somites 4 and 5) is broken down into mesenchyme, the more anterior somites 3

TEXT-FIG. 6.

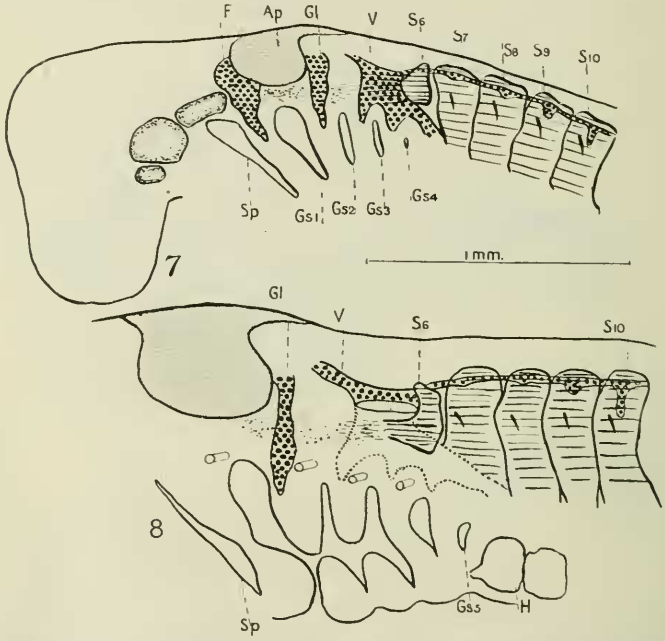


Series of diagrammatic reconstructions of embryos of the lengths of 4·5, 5, 6, 7, 8, and 10 mm. drawn to the same scale. The rudiments of the facial nerve are joined by a chain line, the corresponding somites of the different embryos by dotted lines.

2, and 1 (which will be drawn off into the service of the eyeball), acquire a more anterior position.

Similarly the more posterior somites, 6, 7, &c., move relatively backwards. By measuring somites in the region of the fifth and sixth, it can be seen that they are stretched and occupy more space along the long axis of the embryo than the remainder.

Text-figs. 7, 8.



Text-fig. 7.—Embryo 8 mm. long. Ventral roots are present from the seventh somite backwards.

Text-fig. 8.—Embryo 10 mm. long. The tenth segment is the most anterior to develop a fully-formed mixed nerve. The vagus is represented as truncated to reveal the ventral portion of the sixth somite, which lies median to it.

Text-fig. 6 shows a number of embryos in successive stages of development, all drawn to the same scale. The corresponding somites of each embryo are interconnected by dotted lines. It will be seen that the somite which laps round the vagus and forms the first permanent myotome in the 10 mm. and all later stages

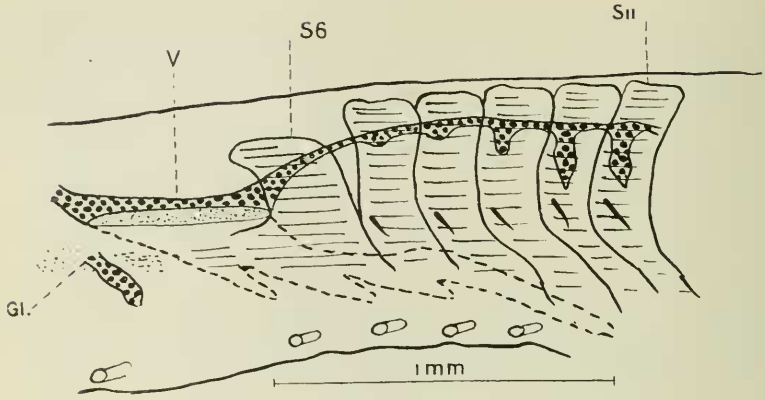
cannot be any other than the sixth, provided that no great migration on the part of the somites has taken place. Several authors regard the seventh somite as the one which gives rise to the first permanent myotome, and this suggests a migration forwards, as described by Braus (**2**). But, as stated above, any relative movement which the somites undergo is backwards and not forwards, and is entirely passive. Text-figs. 7 and 8 are reconstructions of embryos in the 8 mm. and 10 mm. stages respectively. The sixth somite is very obvious, with its anterior margin drawn out and indistinct, anterior to which there are remnants of muscle-fibres of somite 5, and the same is true of the 20 mm. stage (Text-fig. 9).

Up to a stage between 8 mm. and 10 mm. a ventral root can be traced to the myotome of the sixth somite. In later stages, however, I have been unable to find it. This is in agreement with Neal (**11**) and Hoffmann (**9**), both of whom state that it disappears. Presumably the sixth somite is innervated by a branch from the next posterior ventral root and somite (seventh), or the two nerves may combine, but I have not succeeded in determining this point.

The fate of the ventral roots of the post-otic myotomes is of importance in determining the posterior limit of the cranium. Cartilage begins to appear in the L stage (Sewertzoff, **17**; Gaupp, **5**). Text-fig. 10 shows a reconstructed embryo about 50 mm. long. Three ventral roots are present, emerging through foramina in the cranial cartilage. The anterior one is very thin and belongs to the seventh somite, the remaining two are stout nerves. The foramina through which they pass become confluent with the vagus foramen, the vagus lying immediately lateral of their point of exit from the neural tube. These two nerves I regard as belonging to somites 8 and 9. These results are in agreement with those of Hoffmann (**9**). Fürbringer (**4**) did not study very young specimens of Squalus, so that it is probable that his *y* and *z* are the same as Hoffmann's *c* and *d* and my eighth and ninth.

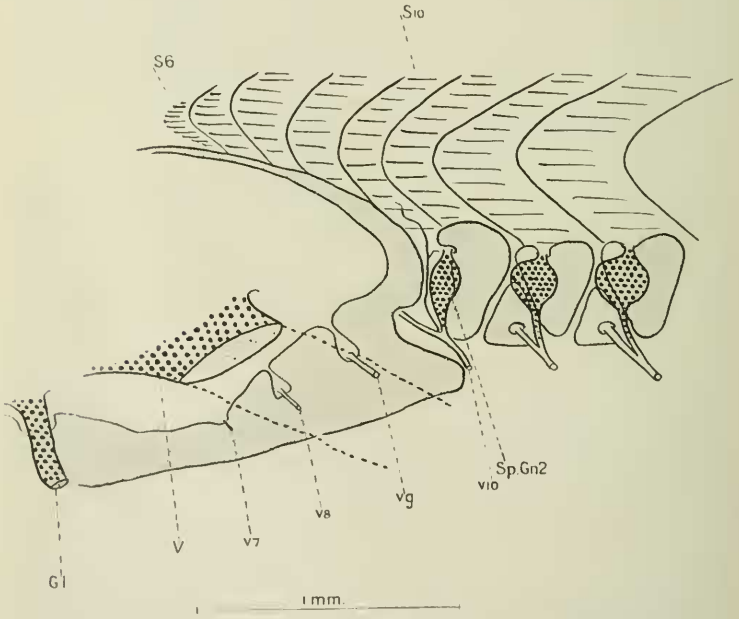
The next ventral root, the tenth, comes out of a deep notch in the posterior wall of the cranium, but behind the occipital

TEXT-FIG. 9.



20 mm. embryo.

TEXT-FIG. 10.



50 mm. stage. View of the occipital region. Three ventral roots are included in the skull, *v* 7–*v* 9, and the next, *v* 10, joins a dorsal root to form the first mixed nerve.

arch so that it is not included in the cranium. Its fibres join those of the spinal ganglion to form the first mixed nerve, branches of which I have traced to the tenth somite. Since the eighth somite is the last of the vagus segments the ninth is morphologically the first spinal or post-vagal (in the case of Squalus included in the skull), and the tenth, which in Squalus forms the first mixed root, is really the second spinal or post-vagal. Rudimentary dorsal ganglia are present belonging to the seventh, eighth, and ninth somites (Text-fig. 9). In Squalus, therefore, there are nine segments included in the skull. Hoffmann (**9**), Sewertzoff (**17**), and others state that there are ten, but since they adopt Van Wijhe's somites, and like him intercalate a somite between those related to the fifth and seventh nerves, the number of their somites from the third backwards are the same as those of Balfour, plus one. Hence their results and mine are really in accordance since we both regard the same segment as being the last one included in the skull, though the numbers attributed to it are different.

As compared with Scyllium Squalus has two more segments included in the skull. But it is interesting to note that in both forms it is the tenth segment (second spinal) which gives rise to the first mixed nerve. It is another proof that homology does not depend on numerical correspondence (Goodrich, **6**).

Discussion.

The acceptance of Van Wijhe's scheme of segmentation renders it necessary that two somites, the third and fourth, should be associated with a single cleft and visceral arch: the spiracle and hyoid arch.

There is in this region one dorsal nerve, the facial, and this Van Wijhe regards as double and representing elements belonging to the third and fourth somites. The hyoid arch he assigns to the fourth somite, and in order to account for the third he assumes that a visceral cleft and arch have been lost. We shall return to this assumption later. Further, he regards the somites from the fourth to the eighth as related to the visceral arch and dorsal root lying in front of them. Now the

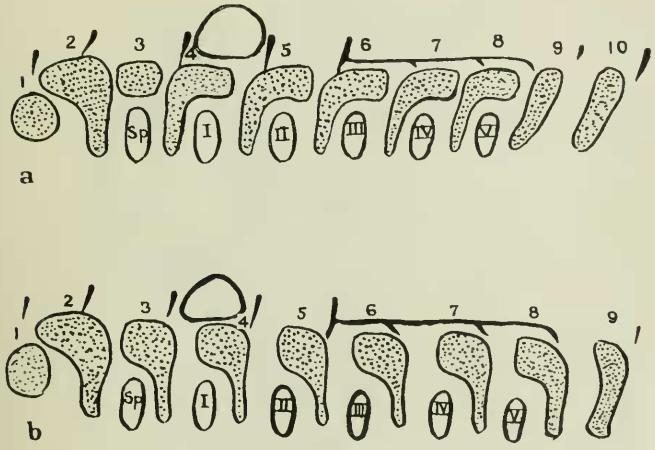
mandibular somite corresponds undoubtedly to a visceral arch (the first) and a dorsal nerve (trigeminal) lying behind it. Similarly the ramus ophthalmicus profundus is situated posteriorly to the first somite. Again, in the trunk region the ventral root of a somite joins the dorsal root posterior to that somite to form a mixed nerve. Therefore Van Wijhe's scheme involves two discrepancies, viz. that in the regions between the mandibular and hyoid arches and between the posterior somite of the head and the first of the trunk there has been a reversal of the relations between somites and dorsal nerves. The first of these discrepancies concerns the trigeminal and facial nerves. The trigeminal is situated behind the mandibular somite, whereas the facial lies in front of the fourth. To be consistent one would have to attribute the trigeminal to the somite posterior to it (third) and the ramus ophthalmicus profundus to the second, but this would leave the first somite without a corresponding dorsal nerve. Similarly, in the region between the trunk and the head, the last branch of the vagus would lie anterior to its somite (Van Wijhe's ninth), whereas the first spinal ganglion is situated posterior to its somite. Not only would the nerves from the facial to the vagus lie anterior to their somites, but they would also lie anterior to their corresponding ventral roots. In the trunk the ventral root is always more anterior than its corresponding dorsal root (Goodrich, **8**). These relations of Van Wijhe's somites are diagrammatically represented in Text-fig. 11.

We see then that this scheme has to contend with serious difficulties, all of which are the outcome of regarding the third somite as having lost its visceral cleft and arch. Let us now examine this assumption. In the first place the missing gill-slit is not indicated by any of the structures which it must have involved and of which it is reasonable to expect that some vestige would remain. There is no trace of arch, cleft, afferent or efferent blood-vessels or nerve. This in itself is significant in view of the fact that the anterior visceral arches are conserved with constant regularity all through vertebrate phylogeny. And even when the clefts disappear they leave traces of

their former existence in the form of blood-vessels, nerves, skeletal elements or modified structures. Then authors are not agreed as to the exact position of this missing cleft. Whereas Van Wijhe considers the hyoid arch as double, Hoffmann and Platt (**14** and **15**) regard the mandibular arch as representing two elements fused.

With regard to the ventral roots there is no question about

Text-fig. 11.



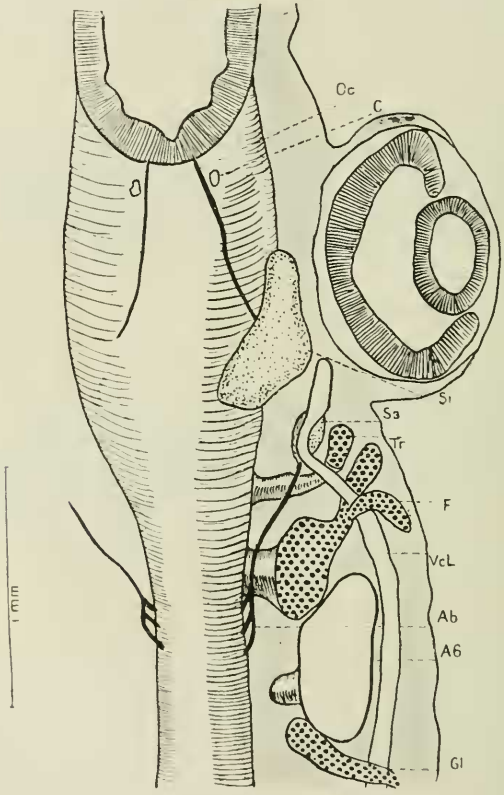
Diagrammatic representation of (*a*) Van Wijhe's somites, (*b*) Balfour's somites.

the oculomotor being the premandibular somite's nerve, and the patheticus, in spite of its curious course, doubtless belongs to the second and mandibular segment. The fourth and fifth somites since they disintegrate have no ventral roots as such (though the fifth is present in Scyllium). To the sixth somite a ventral root can be seen up till about the 10 mm. stage.

The abducens has usually been regarded as the nerve of the third somite and therefore as the ventral root corresponding to the facial. It certainly innervates the external rectus muscle, but Neal (**12**) states that in Squalus this muscle is of composite origin, consisting of elements derived from the mandibular as well as the hyoid somite.

The abducens is held to arise from the neural tube by many roots ; according to Neal four, corresponding to Van Wijhe's somites 3, 4, 5, and 6. I have been able to discern three roots which in a 23 mm. embryo arise not very far behind the facial

Text-fig. 12.



Ventral view of an embryo 23 mm. long to show the origin of the abducens nerve.

(Text-fig. 12). In earlier stages their origin appears to be slightly more posterior. It has been suggested that the hypoglossus and abducens roots form a continuous series, implying that the abducens is a compound nerve derived from elements belonging

to three or more segments, but even going by topographical relations alone it is not unreasonable to regard the abducens as being the genuine third ventral root. At any rate I do not see that the condition of the abducens furthers the assumption that a gill-slit has been lost. If Neal's contention is true the whole question of the eye muscles innervation and segmentation will require revision.

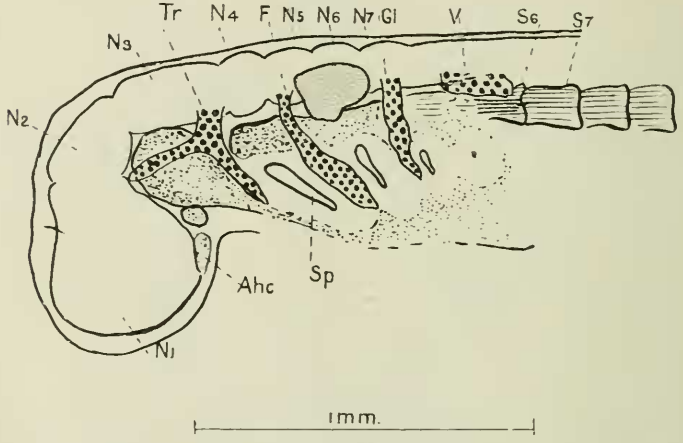
Lastly, one more train of thought has been brought to bear on the supposedly lost organs, and that is the question of the relation of neuromeres to the other segmental structures.

Neal (**11**) describes seven neuromeres, of which the first corresponds to the anterior head cavities with the olfactory as its dorsal nerve : this is, of course, assuming that the anterior head cavities have the value of a somite anterior to the premandibular somites. To the second neuromere correspond the ramus ophthalmicus profundus premandibular somite and oculomotor. The third or cerebellar neuromere later undergoes subdivision (which Neal regards as secondary) and to it belong trigeminal, patheticus, and mandibular somite. The next dorsal root, the facial, arises from the fifth neuromere, and this led to the idea that the nerve of the fourth neuromere (which has none) has disappeared and that it was this nerve which was related to the lost gill-slit. To the sixth and seventh neuromeres belong the glossopharyngeal and vagus, though their topographical correspondence has been lost. The glossopharyngeal appears to arise from the seventh neuromere, and the vagus behind it ; but this is explained as being due to the pressure of the auditory sac and relative shifting of the elements of the neural crest and neural tube. These relations are shown in the embryo (6 mm.) reconstructed in Text-fig. 13.

If it be granted that neuromeres have a primary segmental value, then it may be said that there is one neuromere too many overlying the hyoid arch ; but that such a segmental value exists remains to be proved. To start with it rests on the assumption that the anterior head cavities represent a somite. These are present only in Galeus and Squalus, but in Amia,

Reighard, and Phelps (16) have described the sucker as arising from muscle anterior to the premandibular somite. Goodrich (7) has produced good evidence to show that the anterior head diverticula of Amphioxus are homologous with the premandibular somites of Craniates, and it is more reasonable to agree with Dohrn (3) that no segmental significance must be attached to Platt's anterior head cavities. Then, supposing that the

TEXT-FIG. 13.



Embryo 6 mm. long showing the relations of the neuromeres to the remaining segmented structures.

subdivision of the third neuromere is not secondary but primary and retarded (which it might be, for the third neuromere is just about twice as long as the following ones), it would be necessary to postulate yet another gill-slit lost, to correspond to the extra neuromere. But perhaps the greatest objection to the segmental value of neuromeres lies in the fact that they are altogether absent in Amphioxus, scarcely developed in Petromyzon, irregular and asymmetrical in Bdellostoma, and that they are best developed in the higher craniates, birds, and mammals (Neal, 13). This strongly discountenances their palingenetic value and suggests that they are neomorphs. And so I cannot believe that the evidence from neuromeres favours the assumption of a lost gill-slit.

The simplest explanation then, that originating from the work of Balfour, is the most suited to the facts: the third somite is related to the hyoid arch and the fourth to the third arch, &c.; somites correspond to the dorsal roots lying immediately behind them, as in the pre-otic and trunk regions, and there are no discrepancies.

In dealing with such a subject as segmentation, the essence of which is a simple and orderly repetition of parts, if a simple explanation can be deduced which does not produce inconsistencies or go against facts, the onus probandi must lie with those who would reject such an orderly state of affairs.

Summary.

1. Balfour's interpretation of the somites of the head is correct and free from the objections which accompany Van Wijhe's.

2. No gill-slit or arch has been lost in the neighbourhood of the hyoid arch.

3. Nine segments are included in the head of Squalus, of which three are pre-otic (first, second, third) and six post-otic. Of these

One (fourth) breaks down completely into mesenchyme;

One (fifth) forms muscle-fibres but later breaks down;

Four (sixth, seventh, eighth, ninth) produce permanent myotomes;

The tenth somite (first of the trunk, and second post-vagal) corresponds to the first mixed nerve.

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